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The Embryology of a Termite.

(Eutermes (Rippertii, Rambur ?))

A Thesis.

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By

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The Embryology of a Termite -

(Eutermes (Ripperti?)) -

Though the Termites must be ranked among those insects which have best preserved ancestral characters, their development has not been studied up to the present time - indeed, it is only within the last few years that we have been enabled to judge of the details of development of any of the primitive forms of insects - The technical difficulties, which the investigator of these forms must meet, are very great, much time being required to obtain any results, especially in dealing with early stages - As Wheeler (24) has suggested, no doubt this has deterred many from working on such material - I have devoted considerable attention to

the early stages of the development of the Annelid in the hope that such a study might throw light on some vexed questions of insect anatomy — The later stages can not be treated in detail in the present paper, but will be described at another time —

× The eggs were obtained in Jamaica at different times, by myself, and by the kindness of Dr Smith and Mr Taylor — I am also much indebted to Mr Taylor of Jamaica for assistance in obtaining material, and to Dr Mr Sutton for many suggestions as to literature — It is a great pleasure to express my appreciation of the constant kindness, and valuable criticism and advice, of Professor W. K. Brooks during my

× The species from Jamaica has been described as Ex. Jamaicensis Rafinesque — There is some doubt in my mind as to the species, hence the mark of question in the title-

work at the fish hatching business — I must also remember here, with each regret for its loss, the inviting and stimulating friendship of the late Colonel Marshall Macdonald, by whose invitation I was enabled to spend some time at the United States Fish Commission laboratory at Woods Holl. Mass —

There are no special chambers for the queen or for nurses in the nests of this species, but the inner parts of the nest differ somewhat from the more peripheral portions — The outer series of passages of the Termitarium being somewhat thicker walled than the inner ones —

The queen is usually found in the interior of the nest, near its base, surrounded by numerous workers and larvae and

not far from the larger eggs - These eggs are collected by the workers as they are laid, and piled up in the passages near the queen without any apparent system - The older larvae also take part in tending the eggs - It is an easy matter to collect the eggs, since they all quite moist and adhere together in masses, in which all stages are to be found, from unsegmented ova to larvae leaving the egg membrane -
The material was fixed with hot water with cold picro-sulphuric acid, and with hot picro-sulphuric, the latter method giving the most satisfactory histological result -

The egg is elongated, larger at one end and markedly

convex on one side — This shape makes it easy to determine to plane of symmetry from the start, since the enlarged end is the micropylar or anterior pole while the convex side is the ventral surface — In the course of its development the embryo changes its position by a remarkable process of evolution like that described for the Libellulids and certain Orthoptera. This must be kept in mind in speaking of the anterior and posterior poles and of the dorsal and ventral surface — As noted above, the micropylar end of the egg is the definitive posterior pole, and the convex side is the final ventral surface —

Dr Hagen (11)† described the micropyles of the eggs of this species as follows: "The micropyles of Zenner's eggs have not

† Numbers in parenthesis refer to names cited in bibliography on back of book —

[illegible] — near the upper pole of the egg, on each side there are from 6 to 8 flat infundibuliform pits, in the centre of each of which, in the middle of the shallow funnel is a tube of smaller diameter going through the yolk-membrane in the direction of the egg pole." — The description must be modified, since I have found that the funnels are not numerous and are grouped on the whole surface — the chorion is the only membrane penetrated by the funnels — The micropyles are arranged in a semicircle on the convex face of the egg, near the posterior end — This semicircle is composed of some 12 to 15 funnels which vary considerably in their arrangement — They may be strung out into a single line,

curving over the ventral surface just
above the place where the embryonic
shield first appears, and extending
up on either side towards the dorsal
surface — Often the furrows at the two
sides of the semicircle are crowded
together while the ventral ones form a
single row — Fig. (1) In some eggs
on the other hand, the median ventral
furrows are crowded, while the lateral
openings are strung out into a line —
In surface preparations the centre of
the micropyle may be seen to be slightly
invested — or Hagen thought he could
see distinctly a bunch of filiform spermato-
zoa inside the micropyle in some eggs
and that on one case he had succeeded
in bringing them out by pressure, but
it is extremely doubtful that what he

can see spermatozoa — Filiform bodies often appear beneath the chorion but though I have looked most carefully through a number of stained specimens I can not succeeded in finding any spermatozoa — The objects in fragmentations are probably folds of the delicate vitelline membrane produced by a parasitic fungus — In surface views of alcoholic specimens, the folds of the vitelline membrane and protoplasmic threads attached to the chorion, at times, seem to be bunches of filiform bodies — When such specimens are crushed, the membrane wrinkles up and looks like bunches of filaments — Eggs of my material from one nest had been attacked by a fungus to such an extent, that

the hyaline cutting the microsphe and ramified in the yolk and need it up destroying the embryo; but Dr Hagen could hardly have mistaken such large objects for spermatozoa —

yolk —

My observations on the yolk were made chiefly on fresh material — It is composed of a mass of flattened polygonal bodies, which are vesicles containing a homogeneous coagulable fluid — These bodies stain deeply in Haematoxylin and Carmine and vary considerably in size and shape — The other constituent of the yolk-mass is formed of oily globules most of which generally collect into one or two quite large drops — When alcoholic specimens

are crushed, the oil globules run together and flow out leaving the yolk-bodies for the most part intact — In such preparations the characters of the vesicles can easily be made out — They are found to have in structure part of them being entirely filled with the homogeneous coagulated substance, which is quite elastic under pressure — many of the bodies are much different from this — They also contain the homogeneous staineable substance, but in addition little oily drops of which there may be only a few or a great number — The greater the collection of these drops the less is the homogeneous material; so that it is often reduced to a fine substratum for the drops in the centre and a thin layer around

the periphery of the vesicle — it is excitable & crush such vesicles so that the oil drops escape through the membrane surrounding the vesicle — Examined in clove oil, or in acetone the yolk has quite a different appearance — In these specimens the oily matter is all dissolved out, even from the vesicles — The treatment with oil often causes the yolk-bodies to fuse into large masses — In sections this is often very marked, such large spaces are formed through the mass by the solution of the oily substances — Sometimes however a section of a single yolk-body is met with, riddled with holes left by the solution of the oil drops which are imbedded in the substance of the vesicle — Figs. (23 & 28) — Agreeing with

Whether some of the yolk or Glatta, we should regard the granular looking yolk-bodies containing oil drops as derived from the homogeneous variety — the homogeneous coagulable fluid of these bodies seems gradually transformed into fatty substances, and these at first being formed in isolated drops, finally fills the whole vesicle — In the way the oil globules and pale clear fluid of the yolk would appear to serve from the albuminous (?) bodies to furnish the germ embryo easily assimilable nutriment — Then yolk-bodies in which drops have collected are prepared for sectioning by the usual methods, chemical changes take place which result in homogeneous fixed masses of stainable (albuminous) substance, and

in the solution and removal of the yolk
matter —
There is apparently no definite arrangement
of the different yolk elements —
There is no peripheral layer of protoplasm
distinguishable before the formation of a
blastoderm —
I have found no segmentation of the yolk
during the early stages of development —

Segmentation and formation of yolk nutriment of the Embryo —

The first sharply marked nutriment of
the embryo is, as in the case with Astacus
& the Orthoptera (Stenobothrus, Stagmomantis,
Gryllus, and Decanthus), a relatively
small disc of closely crowded cells at
one pole of the egg — since the

history of the origin of the embryonic area has not been worked out. I have studied, with special care, the segmentation and the changes in the blastoderm cells on the surface of the yolk which result in the formation of the embryonic rudiment.

The questions which I have endeavored to answer are: Is the area formed immediately during the segmentation by cells wandering directly to their places on the surface, or the point where the area is to be? Or is a blastoderm first formed as a result of segmentation, and then the area formed from its cells? Again, if the latter is the case is the embryo the result of a simple multiplication of the cells of a restricted area of the blastoderm, or is there some other factor present in the formation of

the axis? The answer to this question is of [illegible] importance, since it has direct connection with the relations that it furnishes the only clue to the understanding of the origin of the meta-layer and of the amnion. I shall try to make clear that a careful study of these changes which take place in the blastoderm is a necessity to a consideration of these later formations.

The position of the polar-bodies marks the dorsal pole of the shell of the egg. I can only refer you to eight eggs which showed indistinctly the formation of the polar-bodies since the nucleus.

When the segmentation nucleus has returned to the centre of the egg after the extrusion of these bodies

they are seen as two little rod-like masses of chromatin surrounded by a small quantity of protoplasm lying at about the centre of the protoplasmic surface' — Figs. 2, and 3.

Later the chromatic beaks into fragments but the little collection remains visible for a number of divisions —

The segmentation nucleus after moving back from the dorsal surface, the first cleavage of the first division in the centre of the yolk, at the intersection of the shorter and longer axes of the egg — Fig. (2). The first spindle lies at right angles to the shorter axis, so that one of the cells arising from the first division reaches towards the enlarged posterior pole, where the embryo will first appear —

the other cell remains near the position which the mother nucleus held — Fig. (3) — At the start there is a decided proliferation toward the future embryonic area — This is brought out better in the following stage, which exhibits two cells in the enlarged end, one in the shorter one and one in the small end — That is, there are three nuclei nearer the posterior than the anterior pole — Fig. 4 — The cleavage becomes irregular with the eight cell stage, one or more nuclei lagging before the time for a typical cell of division — For several divisions there is a slight predominance of cells in the larger end of the egg — For instance, one egg has four nuclei in the end, one in the shorter end — three in the anterior end, while

another are found in the posterior end
four in the opposite end — Fig. (5).
Generally during the early stages of cleavage,
there are three or four more cells in
the larger than in the smaller end of
the egg — after four or six cleavages,
division, though the number of cells
in the posterior is slightly greater than
that in the smaller end, owing to
the more extensive surface, they have
taken up positions at about equal
distances apart — It will be noted
that I speak of the nuclei with the little
masses of protoplasm around them as
true cleavages, or cells — So far as can be
determined there is no protoplasmic continuity
between these cells — Later when the
embryonic disc begins to differentiate
is established between its cells, but

now that there is no part that the blastoderm cells themselves or the yolk are connected with one another or with the yolk-cleavage of the central surface of an egg at this stage there may still be equal distribution of the nuclei on that side, and the same is found to be true of all the cells in the eggs — figs. 10, 11, 12, and 13 — most of the cells have now reached the surface, there being only a few in the yolk which are at about equal distances apart — in properly prepared material, the single flat cells and lead to the appearance of the embryonic disc can be most distinctly traced in entire transparent eggs studied in clove oil, cedar oil, or balsam — The following description refers chiefly to specimens studied in

this way, and at a time through certain stages — I have already stated that the various stages are mixed together indiscriminately when collected — hence the series illustrating the growth of the disc, are here picked out of a great mass of material — there can be little doubt however that I have figured a typical series, for the figures are based on a great many specimens — since the first rudiment of the embryo is formed from the surface cells alone, the few yolk-cells may be neglected in the description — The cells on the surface of eggs with more nuclei than three just described are slightly more numerous in the posterior end — In many specimens it is evident, that the cells of this end are dividing more rapidly than are those in the other end — the nuclei

are grouped in two's in the surface of each specimen, and are frequently to be found at all points in the surface, in the act of dividing; but it is in the enlarged exterior end that the greater number of dividing nuclei, and pairs of just separated cells appear- ings (8), (8), and (9).

Figures (10) and (10a) represent the ventral and dorsal surfaces of a somewhat older egg than that just described — The number of cells is now greatly increased, especially in the posterior end — The nuclei are still evidently grouped in twos, and some are seen in the act of dividing — The anterior half of the egg contains [illegible] nuclei — It is to be borne in mind, in fact that I was for a long time puzzled that their absence was only apparent, and

due to improper handling of the material — This can not be, however, since special care was taken to prick that end of the egg, & some penetration of the staining fluid, and since the nuclei, which do appear in both ends of the egg, stain my satisfactorily — There is no reason to believe that all of the nuclei are not stained in these stages — It is important to note, in figs. (10) and (10a), how far the immature nuclei of the posterior side extend anteriorly — In both the ventral and dorsal surfaces a considerable area is covered by nuclei, at no great distance apart — A cap of nuclei (cap) is thus formed over the posterior end of the egg, which stretches forward almost to the shorter axis — The nuclei are

not grouped around any one center —
The egg shown in figs. 18, 18a and 18b
are more alike and so therefore somewhat
older than that exhibited in the preceding
figures, but there is also a difference
in their arrangement — In fig. 18 of
the central surface the cells of the
anterior end are seen to be closer
together than in fig. 18, though their
number has not increased much — The
anterior edge of this area is more
distinctly shown than in the foregoing
stage and is nearer the anterior end
than the shorter axis of the egg — The
dorsal surface fig. 18a is fuller of cells
than in the last stage — At its extreme
posterior limit the cells are crowded
closely into two or three concentric rows,
rather sharply separated from the rest

of the cells of this surface — This can not be shown better in a drawing, though it is much more distinct on rolling the egg — These rows of nuclei mark the posterior edge of the area of short columnar cells, so prominent a feature of the ventral surface — It will be seen from these facts that this area, while quite extensive, is decidedly less so than in the preceding stage — It is not marked on the ventral surface, but extends around on either side and over the posterior end toward the dorsal surface — Fig 18 shows this from the side — Fig 19 gives a ventral view of an egg at about this stage, in which the nucleated area terminates abruptly at the pole of the egg, and at the side is seen to thin out gradually

as in the black figure - fig (18) -
In older specimens the nuclei are still more closely crowded, and form a more and more distinct area, which becomes gradually more restricted in extent -
Figures (15-18) illustrate this point, and it is also evident in these figures that the nuclei of this region are of the same size as those elsewhere on the surface - Figures (14) and (14a) of the same egg, and fig. (15) (16) and (17) exhibit a stage in which the posterior and lateral borders of the nucleated area can become quite sharply defined - This region is now very distinctly outlined, and may hence forth be spoken of as the embryonal area or germ-disc, though it is only this until it be reached the stage represented in fig (21) or (22) -

In fig 2, three fowls are represented
enclosed the embryonic disc is seen
to be a well defined area of nuclei
which are quite flush enveloped — Careful
study shows that they are about the
size of those in the surrounding
blastoderm — Anteriorly the disc is
not so sharply delimitated, as on
the rest of its circumference, and this
is true until a late period in the
formation of the disc, as will be seen on
referring to the figures of later stages —

The facts just reviewed appear to me
to prove that the embryonic disc is not
formed directly by the segmentation of
cells wandering inward from a predetermined
point — The evidence seems to indicate
also that the disc is not the result of

rate active cell multiplication in a certain area of the blastoderm, but that there is a concentration of cells of the blastoderm toward the place where the first rudiment of the embryo appears — This is shown in the whole series of stages figured, and is brought out vividly by comparison of figs (12, 13, 15) and (20) — The diminution in the area covered by nucleated non closely crowded than elsewhere on the surface is very marked from fig. (14) to fig. (15) — in fig (14) it spreads over the whole ventral surface of the posterior end of the egg, while in fig (15) it only covers one half of this area — The best proof of such an origin for the disc is found in a number of stages like those figured, showing the

gradual concentration of the nuclei from all sides toward the embryonic area— The disc is early outlined as a result of this process, especially along its exterior border: but for some time after this it occupies a larger area than is the case when it is completely formed— This is significant since, if it were merely a question of cell multiplication the boundaries of the disc would be quite sharp & gradually extend out from the centre, and not contract toward it— The nuclei of the disc in all of the stages are of the same size as those of the rest of the blastoderm; and this is true in later stages, as in fig. 18, where the disc is formed and the amnion has made its appearance— High powers show no distinction between the cells of

the disc and that of the blastoderm outside of its circumference —
This fact evidently supports the view here advanced that the disc is formed by a segmentation of the blastoderm cells — a rapid multiplication of cells within a restricted area should, it seems, soon lead to a marked difference in size between the nuclei within that area and outside of it — Dividing nuclei are found all over the central surface of the posterior end of the egg, during the stage leading to the formation of the disc; but they are not more numerous in the region finally occupied by the disc, until a comparatively late stage in its development represented by figs. (6) and (9) — At so late a stage more dividing nuclei would be expected in this area, since the cells

dorsal crenule rather closely crowded — It must be remembered though that the area occupied by the disc at this stage is still further reduced later — (see figure) The first rudiment of the embryo is certainly not formed from a number of discrete centres as in the decapods and in certain insects — The concentration leading to its formation is, from the first, most marked on the posterior border of the disc which early becomes sharply defined, as the cells there together in concentric rows from the dorsal surface — The lateral edges are next involved, but much later, when the disc is otherwise well outlined and its cells are quite closely crowded, the cells of the anterior end have not yet drawn together — Figs (34) and (35) — When the amnion is about to close over, the cells

of the sub Germ drawn together and become incorporated in the disc —
I can not determine whether the concentration is accomplished by the migration of independent amoeboid cells toward the embryonic area or whether the blastoderm is a continuous membrane of cells which contracts toward that point — The latter may be the case, though it is not clear that there is protoplasmic continuity, except where the cells are crowded in the region of the disc — It is however often difficult to establish continuity much later, when there can be no doubt of its existence in the reverse —

A less marked concentration of the surface cells has been observed in other insects, notably by Patten (19) fig. 5. B III and by Wheeler

(23) figs 63 and 64 and 66 and 68) resulting in a close approximation of the cells of the embryonic area — In the limits where the embryo is a comparatively small disc in its first appearance, the concentration to establish the disc is an especially marked process — Mr Minnich has discovered a similar method of the formation of the embryonic rudiment in 'Isoporke' — His figures (16 figs 7, 8, p. 19) and (50–52) show how the germ-band is formed in these crustacea, by a concentration of the surface cells towards the ventral side of the egg — We find an intimate connection between this phenomenon and the formation of an under-layer and my observations on the limits of the head will be a powerful counter

conclusion for it — hence the detail with which I have described the process —

Sections show that the disc, in its early stages, is typically one layer of cells with a few scattered yolk-cells beneath — as the disc becomes more distinct from considerable displacement is shewn in the nuclei of this layer, It should be noted that this take place at all points in the disc, laterally as well as from the middle line — due to the concentration of the cells towards the centre — Hence some cells are crowded beneath the surface as is shown in fig. (23), which is a cross section of a very young disc, fig 6, — the smoothing of course more marked in some stages than here, between some the surface fig. (22) concentration. has been carried to an extreme —

form the disc a central layer thick in section and its nuclei exhibit all stages in the karyokinetic process beneath the surface — Fig. (24) — Sections of the embryonic area in which the disc is first distinctly outlined, show also that the nuclei are dividing in place & separate cells from the inner surface — Fig. (23) — These cells subserve in the inner layer of the disc —

Under-layer and Embryonic Membranes —

Figures (25), (26), (26a), (27) and (28) show light on the processes now to be described — Around the centre of the disc the cells are now more closely crowded than elsewhere on its surface, and form a conspicuous dark spot — The figures also exhibit another circular line of the first trace of the amnio-thoracic

pilot, which appears from the surface as a dark semicircle of crowded nuclei arranged concentrically along the anterior edge of the disc — the rest of the disc being much lighter from the surface the nuclei being further apart — the figures represent several stages in the growth of the central dark spot and in the increasing distinctness of the posterior semicircle of nuclei — sections through these stages, and three great succeeding and immediately following, taken in connection with what has been learned from surface view, give interesting data as to the formation of the under-layer and the amnion —

as whether formed in working with sections through these stages are very difficult to obtain — It is impossible to get good views of the entire egg without adopting the

tissue, and not altogether satisfactory method of staining each section before cutting as Schiefferdecker suggests (?) — The method which I have used most & last first described by Dr Jno Patten — It is rather a slow process, but most satisfactory — As such it can not be dispensed with, in handling such small objects, and Dr Patten has certainly done a great service in publishing it — In applying the method of staining the early stages of the Termite embryo — I break off most of the yolk in clove oil with sharp needles under the dissecting microscope, and stick the portion to be sectioned in a piece of rolled paper — After imbedding in paraffin, the paper may be stripped off, leaving the object just as suitable for cutting — It is possible in the case

to their sections of quite early discs, in any plane and of any desired thinness — enough yolk adhere to the disc to make plain its relations to the interior of the egg —

I have studied the origin of the under-layer with special care, on account of the recent conflicting results of Weber[12] and Heymons[13] in regard to its formation in the Orthoptera — In the Gryllidæ there is no particular imagination — The under-layer begins to make its appearance at an early stage in the formation of the disc fig. 18 and 19, when its cells are not very closely crowded — At this period, at irregular points in the embryonic area, lateral as well as median, some of the cells, as has been said, are pushed below the surface by the concentration of the

blastoderm — Other cells are separated from the under surface of the blastoderm, at this period, by segmental division of its nuclei here and there —

As the process continues the under-layer constantly gains in increase — Its formation seems due chiefly to the concentration of the disc, and when this has reached the stage represented by fig. 27 the under-layer cells have, for the most part, collected into a plug projecting into the yolk — From the surface, this plug appears as a darkened area of crowded nuclei — A sagittal section of a disc of this age, shows the plug quite distinctly — It also seems in this section that the under-layer cells are not confined to the plug, but are being pushed below from the ectoderm posterior to the plug, as far back as the hinder border of the [illegible] fig. 27 — A cross

section of the blastoderm round the region of the area, at this stage, fig. (30), when compared with figs. (31) and (32) cutting the same region of younger discs, (31) of stage represented by fig. () and (32) of that shown in fig.) show that the plug has grown inwards by the gradual addition of cells from the ecto-derm — both surface views and sections of this stage agree in exhibiting no fasciculo investigations — as to contrary, it is as I have stated: the under-layer arises at all points in the germinal disc, as a result of a concentration of the embryonic area and of the tangential division of its cells — the formation of a mesentoblastic plug is apparently a further outcome of the concentration — (see Mr Minot on the formation

of the under-layer in Exocoetus (b) —
Preparations of a series of discs, after the
under-layer has much become curved
into a plug, illustrate the growth of
this collection of cells — Figures (25), (27), and
(33–35) exhibit, in surface view, the
gradual extension of the plug, up to the
time when the amnioserosal fold has
grown well forward over the disc —

I have devoted much attention to the early
history of the embryonic membranes, on
account of the general interest which their
formation excites — When the amnio-
-serosal fold is first clearly defined, as a
fold, in section, it appears from the
surface as is shown in fig (34), as a semilunar
fold along the posterior border of the
embryonic disc, extending forward to

near the anterior end on either side — Sagittal sections of this stage make it plain that the inner or amniotic layer of this fold do not at present distinguished from the ectoderm of the germinal disc — fig 30 It is of the same thickness as the ectoderm and its nuclei are arranged in the same way, nuclei of amnion — The outer or serosal layer of the fold, on the other hand is quite different — fig (36) It is a thin membrane of much flattened cells, with nuclei comparatively far apart — This is however not the first stage in the formation of the amnio-serosal fold of the Annite — Earlier stages before a fold can be made out in sections, it position is outlined on the surface of the disc — When the medullary plate first appears in surface view, the embryonic disc is quite sharply marked out from

on its posterior border — fig. 25 — as has been
said, it is along this border that the
primitive streak appears — it is the
nuclei in this edge, which have the
same character as those of the rest
of the disc or of the extra-embryonal
blastoderm — fig no indication of the
fold about this time — In a
slightly older disc fig 27 however the
posterior border is seen to be formed
of a semicircle of closely crowded concentric
rows of nuclei, which stands out
very distinctly in surface views —
Figure (28) represents a later stage than
this and one before a fold can be
distinguished in sections —
Sagittal sections of discs in these stages,
esp fig. 30, teach that the posterior
margin, corresponding to the dark

cuticle on the surface differs from the rest of the disc only in a somewhat greater thickness fig (37) —

It is the posterior thickened margin, & lobes, which are folded over in fig (36) and become the amnion —

It will be noted then, in reference to the origin of the amnion, that it is a portion of the embryonic disc, and that it is indicated as a thickening of the posterior margin of the disc, before it folds over & becomes the amnion —

This agrees essentially with the figures which Bonnet gives of Lacerta (6) figs (42) & (43) of plate II, with Kastschenko's description and figures of the Chrysemys (9), with Will's of the Aves (35), and with the results of most other authors; though all are not agreed to regard the amnion as a fold

of the embryo — It is or it may it is certainly a portion of the first rudiment of the embryo of the Gnnite — I have reserved a final section of this paper for a consideration of the origin of the membranes —

Preparations of eggs illustrating successive stages in the closing of the amniotic cavity show that this is accomplished by the single, semilunar tail-fold from the posterior end of the disc — There are no separate lateral folds, nor is there any head-fold — In a series of specimens the membranes are found extending further and further forward over the disc — Finally the amniotic cavity remains open at only a single point at the anterior extremity of the disc, the closure of

which opening completes the process —
Figs (35) (36) (39), (40), (40a) and (41) —
During and just after the closure of the
mouth the amnion is not distinguish-
-able from the ectoderm of the germinal
disc — It is quite thick being composed
of cells crowded into two layers, and its
cells look like and act like those of
the ectoderm — When the amnioserosal
fold has once arisen, the enclosure
of the disc by it appears to be due
simply to the multiplication of the
cells of the amniotic layer —
A sagittal section of an embryo just
after the closure of the amniotic cavity
shows this similarity strikingly fig. (42) —
Comparing fig (41) with figure of earlier
stages, it is evident that considerable
changes have taken place in the shape

of the embryo — The disc has now grown longer — It is about twice as long as broad and while the posterior end is enlarged and rounded the anterior extremity is distinctly pointed — The cells of the disc and of the amnion have become much smaller from repeated divisions, while those of the area have long since ceased to divide and are now very large — The capital section just opened 5, fig (92), brings out well the condition of the lower-layer — The plug of cells which forms the layer has now become very prominent and lies beneath the anterior portion of the disc — It does not extend quite to the anterior extremity of the embryo and falls somewhat short of the posterior end —

The growth of the germ-band, its segmentation
the appearance of appendages
and
— Revolution —

A series of embryos from the stage just described & one exhibiting the first traces of segmentation throw some light on the method of growth — This is accomplished by the hind end of the embryonic band pushing back from the posterior end of the yolk mass, just beneath the serosa, while the head end remains fixed — until it reaches about half way over the posterior pole, no marked change takes place superficially except an increase in length and breadth — Figs 2 and 3 — The anterior end however becomes gradually less pointed — When the posterior

end of the band has pushed around the yolk mass, and has struck the flattened basal side of the egg. The embryo forms a U shaped cap over the enlarged end of the yolk — Fig 20 — At this time the band is still unsegmented — Posteriorly it terminates as before in a rounded extremity — The anterior end however has gradually undergone considerable change — From being a narrow pointed tip of the band Fig 17, it first widened into a square end Fig 18 and finally spread out over the yolk mass and laterally Fig 19, until now Fig 20 this region has become the most prominent part of the embryo — Anteriorly just in front of the place where the mouth & stomodaeum appear a slightly marginal — On either side it extends up on the yolk in a broad lobe with rounded borders. Fig 20 —

In section of three stages named just before apparent — the under layer is gradually thinner from the extreme — to the extreme layer of the embryonic area elongates the under layer cells multiply and form three protrusions (fig 4) — the fold which in earlier stages marked the outline of the embryo now ends in front at the base of the cephalic region (fig 7) (8) — the cephalic region is thus seen to have been formed entirely by the spreading of the ectoderm anterior to the medullary plate after the closure of the embryonic membranes — as the germ-band has elongated the under-layer of germ cells thickly back, apparently largely as a result of the multiplication and rearrangement of its own cells — (fig 6) and (7) — the ectoderm germ cells are widely than the lower-layer which does not extend quite to the posterior

end of the embryo during its elongation — When the posterior end of the head is pressed down the ectoderm of the head is collected into the mesoderm — Fig. 11 — it forms only a comparatively thin layer anteriorly where it is quite distinct from the ectoderm — At the other end of the embryo however I am not certain, as yet, that it does not unite with the ectoderm below and with the under-layer — it is possible, I think that will be the case — I have not followed the differentiation of this layer further, but may state that the endoderm is not found as a distinct layer until after the appearance of segments — The origin of the endoderm from yolk-cells is not possible, since there are only two layers of

there is the yolk and much earlier than are larger than the entoderm cells are — Fig (8)

These sections also exhibit well the changes which take place in the growth of the amnion — up to the time of the closure of the membrane the amnion was seen to be sinking like the ectoderm of the disc — viz at the germ-band elongate posteriorly and at the cephalic region touches but anteriorly, finally the cells of the amnion continue to multiply the membrane is gradually stretched the cells arranging themselves in a single layer — This takes place first at the anterior end the posterior end for sometime retaining its early appearance — Fig (2), (7) and (8) —

The first trace of segmentation and appendages appear suddenly, at about the last stage described, when the germ-band has become a U-shaped cap over the posterior end of the yolk mass. The earliest segmented band is the jaw-band in which the antennal are just noticeable as backward processes of the cephalic lobe post-oral in position – Figs. (79) and (92) – The first maxillary and first thoracic segments are alike – The other anterior segments are indistinct and the sub-jaw is long and unsegmented – The anterior segments through the first thoracic appear then to have arisen almost simultaneously – There are no macro-cruste as I state described for Stenothoe and other forms – (8) and (9) – Later

embryo show a progressive increase in length and complexity of the germ-band. When the head has pushed forward along the surface of the yolk almost to the anterior end of the egg three additional segments have been added — Fig. (5) — These are the two posterior thoracic segments and the first abdominal — They are added successively one before back, as in an embryo in which the first thoracic & the last segment distinguishable, there with an indistinct second thoracic beside, and yet a third bit with three distinct thoracic segments and an indistinct abdominal — In older tracks more abdominal segments are successively added posteriorly — The deep inter-segmental grooves separating the first

and cleavage segments is a peculiarity of this stage — Later when the appendage first makes its metachronic appearance —

The head of such an embryo is shown from the dorsal surface in figure 31 in an early stage of folding off from the yolk — It will be remembered that in the first appearance of segmentation the cephalic region was formed of two broad lobes which had arisen as appearance of the anterior end of the germ-disc — Now, the lateral margins of these lobes bend (or rather roll) upwards and fold over towards the middle line — This is the beginning of the formation of a head-cavity — In fig 31 the cephalic lobe is seen to have formed a sort of pocket between its dorsal and

ventral folds — In older embryos this process is continued, the lateral folds of the head again finally meeting over the dorsal mid-line and enclosing the head-cavity — The antennary metameres are included in this folding; and hence later, their cavities are continuous with that of the head — At an early stage in the formation of the head, the labrum appears; and, as far as I can determine at present, it is from the first an unpaired, median outgrowth, just over the mouth opening — This median fold appears to assist in drawing the head together into its definitive compact size and shape —

The embryo has now attained a stage like that figured by Brandt for Calopteryx in fig. (1) of the paper (3) — It is

more like Corpa lunare, since unlike the embryo of the Cheilostomid it is not surrounded by the yolk — (I must refer here to Graber's figures of the development of Steenstrupia, which is remarkably similar to that of the Termite, as described here in all of the general features, though no "evolution" has been described for Steenstrupia.) In the Termite when the germ-band has grown along the surface of the yolk to the anterior end of the egg, the anterior portion of the abdominal region sinks slightly into the yolk — As the embryo continues its elongation, the bend in the abdominal region becomes more marked, and the tail-end of the band sinks ventrally towards the head until the stage represented in fig (5·2) is reached — The appendages have become prominent —

The 1st maxillae are foliate, and the 2d pair less markedly so — In the abdominal region 10 well marked segments have appeared and each bears a distinct pair of appendages — (no abdominal appendages are figured by Brandt at the corresponding stage of Calopteryx — some of Prater's figures of Stenobothrus exhibit such marked rudimentary appendages in the abdominal region —) —

From this stage until evolution the embryo undergoes no change of shape or position, but the sides of the head grow dorsally somewhat, and the appendages elongate considerably —

Revolution is accomplished as described by Brandt (3) for the Libellulid; and when it is completed, the head of the embryo has shifted up

to the anterior end of the egg, while the tail-end lies beneath the micropyle — The ventral surface of the embryo is now on the micropylar side of the egg, as at first up to the closure of the embryonic membranes —

I can not, as yet, studied in detail the stages after the appearance of the appendages, but will state, in regard to the origin of the central nervous system, that it is evident from sections that it arises from neuroblast cells, as Heider and Viallanes have described for the Orthoptera — In the Termites the process is very marked — I may say, with respect to the reproductive organs, that there is no trace of them distinguishable in the embryo within

the egg, or just after leaving the egg membranes — Fritz Müller (18) found that it was impossible to detect any trace of sexual organs in the soldiers, and workers of certain species of Termites. This is true of the species from Jamaica on which I can worked, (Eutermes - (Rippertii ?) — a careful study of sections of both the larvae and adults of these forms fails to reveal any trace of sexual organs — I am now investigating this question further —

× The Jamaica form is in some respects different very much from Rippertii, hence I can placed an interrogation mark after the specific name.

— The integument —

Recently the origin of the underwings so
that we consider as the most primitive
insects, the Orthoptera, have been carefully
studied by two well known investigators,
who have reached quite contradictory results—
Wheeler, in his "Evolution of insect embryology"
has devoted considerable space to a
review of the question — His conclusions
is expressed as follows: "It follows from
the observations here recorded, fragmentary
as they are in many respects, together with
Graber's observations on Stenobothrus, that the
Orthoptera can no longer be regarded as
rose de lignée, so far as the formation of
the germ-layers is concerned — In all the
families of the order, save the Acrididae,
the imaginate gastrula has been found and
there can be little doubt that the investigation

who it is intimately as to study ontogeny of
the family will find in this essential
the same process of germ-layer formation —
The view is now pretty generally held that
in the insecta both mesoderm and endoderm
arise from a median longitudinal furrow
(the inner layer sometimes only the entire
cephalic lobe in the oval and
anal region of the germ-band) and
that the vitellophags, or cells left in the
yolk at a time when the remaining cleavage
products are travelling to the surface to
form the blastoderm, take no part whatever
in the formation of the mesoderm, but
degenerate in situ and finally undergo
dissolution ".

I am very much to obtain a copy of Heymons'
study of the germ-layer formation of Periplaneta
and Dimastes (19), but the conclusions are

appeared in abstract and on no follow.
The epik-cells take no part in the formation
of the embryo — There is no free proliferation
process in the middle-layer since from
all parts of the embryonic area — When a
typical 'gastrula invagination occurs, as in
most insects it is to be explained as
a simple mechanical process caused by an
aggregation of cells at one point — The layer
generally known as the mesoderm is in
reality only mesoderm, the entoderm
appearing relatively late and arising from
the ectoderm of the dorsal and ventral
invaginations —
In Crustacea plainly accord rather with the
latter view than with Weber's, which is the
one more generally accepted — The termite,
which is certainly as primitive as any other
form hitherto described, exhibits no gastrula

imagination — I can show that the under-layer begins to appear in all cases on the embryonic sediment, in an early stage of its formation — The play of lower-layer cells, which become so prominent as the germinal-disc grow more distinct, is apparently the outcome of secondary conditions — The relation of such a method of formation of the under-layer to that usually described in insects is interesting to consider — The process does not appear to me to be derived from an invagination, as a closed gastrula — It is rather a method of delamination, when there is a further tendency for the lower-layer cells to collect towards the middle line — A similar method has been described in Arachnids and Myriopods, and all of them must be taken together if one might to form an opinion — I should not however

agree with him in regarding the ringmate
structure as simply a mechanical process,
but should prefer to look on it as
arising by natural selection from the method
of elimination just described —
Weber does not claim to have made a
special study of this question but, since
his opinion agrees with what has generally
been thought to be true, further comparative
research would seem necessary, before we
finally decide that the so called ringmate
structures of insects are secondary phenomena —
I am not inclined to regard the question
settled by what I can find in the literature
alone, but think that the Orthoptera, and
other primitive forms should be again studied
from this point of view —
As to the evidence of the fossils I must
say that it appears late, after the

germ-band is segmented — the yolk-cells can take no part in the formation of the layer cells at an early stage, before the closure of the amniotic cavity has become very large and include the cells which later form the mesoderm —

— The Amnion —

The origin of the amnion, whose appearance in the insect-embryo is perhaps the most striking peculiarity of the development, has been much discussed — At the present time however the question is still quite unsettled, opinions being divided chiefly between two views —

Wheeler [2] supports a purely mechanical theory and holds that the amnion first made its appearance in the Hexapoda. Korschelt and Heider [3], on the contrary, have

listed incidentally once in the text-book & on account — which were the structures & phenomena likened to Amphioxus — the viscera, which has received more attention than that of Ayers[20] and Brooks[21] maintains that they are the main type of development among insects — "The intestinal type is best seen in the Libellulidae, which represent the direct connecting link (ancestral) with the phenomena exhibited by the Amphioxus, and hence must be regarded as the more primitive type — Judging from Heider's remarks in his monograph on Hydrophilus[22], no genetic relationship is meant here between the developmental type of the Amphioxus embryo and that of the insect, but the treatment in the text-book certainly suggests strongly such an interpretation —

Ich nenne die Richtung, die gerade
hinter der Spitze, welche
sich bildet, wenn die
Spitze, sich zu wenden, in die
folgende Form — Wir haben oben gesehen
dass bei den Spitzfedern die fortschreitende
Längenwachsthum des Kinnstreifs derselbe in
seiner Mitte eingeknickt und in das Innere
des Eis versenkt wird — In dieser Einsenkung,
welche wir nun zunächst durch das
räumliche Verhältniss zwischen dem
langgestreckten Kinnstreif und der zunächst
Form entstanden zu denken haben,
werden wir, wie dies schon Fraser
andeutete und Will neuerdings ausführlicher begründet hat, den
Ausgangspunkt für die Entwicklung
der verzweigten Kinnstreife der Schlundsäcken

zu suchen haben – Wir werden demnach für die Entwicklung der insectenkinnbacken die Form der Invagination als die ursprüngliche betrachten –

The account is apparently based on Heider's[12] discussion of the subject in his monograph on Hydrophilus – It is a modification of Wilh[175]'s view, against which in its original form, Haber, in a more recent paper[9] has so ably objected, brought forward strong objections –

Since the publication of Kowalevsky and Heider's text-book further investigations have shown that a number of the Orthoptera besides Gryllotalpa, as well as the Termite, exhibit essentially the same phenomena of development as the Hymenoptera – It was

seems evident that there are no grounds whatever for regarding the method of development followed by the Cephalobid embryo as one with more primitive than that of ordinary cyclus or the Annelida — There is some reason for believing it to be more secondary than any of the, since the embryo is of the immersed type — a superficial germ-band is usually characteristic of Arthropoda, and when we find one sunken into the yolk there is cause to believe the primitive has been secondarily — Among the insects, most forms, and especially the Orthoptera and Annelida which are probably exceptionally primitive agree in having superficial embryos — The exceptions are rather marked and are found among the Hymenoptera, the

Termites and the Libellulids — In the Aphidiotera the immersed position is admitted to be secondarily derived from the superficial or protective position or some other source — It appears to me most probable that the same is true for the Libellulids and Termitera with inner germ-bands — Hence I should regard the superficial embryos of the Orthoptera and the Termites as more typically primitive for insects, and should expect to find among them the best examples of the ancestral method of forming the amnion — Similar causes may have brought about the "doubling-up" of the myriapod embryo into a yolk and the origin of the membrane in insects, but the Libellulids do not appear to represent the latter process

in the most primitive condition — it seems probable that the ancestors were first to cover a superficial germ-band, and that the Libellulid and Lepidopteran embryos have later taken up an immersed position, while our insects have retained the primitive superficial one —

As to the cause assigned for the sinking of the myriopod band into the yolk, the resistance offered by the spherical chorion to the growth of the elongating germ-band, expressed as "das sämtliche Eiseverhältnisse zwischen dem langgestreckten Keimstreif und dem rundlichen Eidotter," it may be observed that similar conditions in the arachnid egg and in that of a fish do not lead to such an invagination — (see also Graber's criticism of the idea

in his monograph on the germ-bands &
insects &c. —

A striking character of the development of the
limbs is the small size of the first
rudiment of the embryo, the germ-disc, when
compared with the definitive length of
the embryonic band — The germinal rudiment
must elongate through the whole length of
the egg and add successively all the
segments of the body before the embryo is
formed — This is equally noticeable in
the case of one of the Orthoptera: but is
here marked in most insects especially
among the more specialized forms of the
group —

how it seems to me that
the limbs and the Orthoptera with a
superficial embryo beginning in a disc.

which must elongate inordinately & attain the definitive number of segments when attained much nearly to the typical number — development for both sexes, and, with both apparent to duplicate of the ancestral insect — The pairs of the Amblycera, the Rhynchophora, the Arachnida, and to a less marked degree the Myriopods show a similar disproportion in size between the primary rudiment and the definite segmented embryo — This may be illustrated by reference to the parts of a nauplius of the adult form —

These primitive forms of insects are also characterized by another peculiarity of interest in the present discussion — The antennae arise very early and completely cover the embryonic thoracic area upon its appearance — We do not know with certainty to what need of the embryo

the amnion as such, and would correspond
to that in its most primitive condition
in the very same mode of origination — I
believe this to be the case and that insects in which
the membrane become permanent and cover over the
embryo instead of as in its growth appear a
secondary condition — of, as is generally supposed,
the amnion were as a protection for the germ-band
against mechanical injury or too rapid evaporation,
it would have been a great advantage for it to
appear at the earliest possible moment in
the growth of the embryo — this moment is when
the germ-disc is established and about to germ-rise
the elongated, segmented embryo — From this time a
superficial germ-band would be constantly exposed
to the dangers mentioned — Hence it seems
reasonable to suppose that the embryo
of the ancestral insects must have been
covered by the membrane at

the early stage in the development — Among Insects some, the Termite and some of the Orthoptera (Stenobothrus, Gryllus &c) have lost retained the method of the formation of the Amnion — In other Orthoptera, the Libellulids, some of the Hemiptera, and many other which the ancestral history is not so well known — in these the Amnion no longer closes over at such an early stage — While a figure of the formation of Blatta and Gryllotalpa (23), Eulabis of Lina (9), Nauclores of Hydrometra (12), and Weismann's Chironomus (24) illustrate this point for superficial embryos — the Libellulids and some of the Hemiptera retain in a modified degree ancestral character — Hence, the much extended closure of the amniotic cavity and the presence of the so called secondary Amnion-fold, together

with the secondary rounded friction of the
fore-hand under fore knee
typical examples of the suitable sinuous
method of development—

Whether Lac recently (or) adapted Epstein's
theory of a mechanical origin for the
arrivers of vertebrates & the insect armour—
Of course the word mechanical is used here
in its narrower sense, signifying the existence
of a few simply stated conditions of
pressure and mechanical strain — The view
must be severely criticised it seems to me
only because of the habitual caution which
characterizes thinkers such and the normal
trustworthy nature of his conclusions —
The theory is clearly stated in the following
quotation ---- The universal fold is
a mechanical result of a local multiplication

of the blastoderm due to rapid
proliferation in a single layer of cells—
There is the vascular area-lipped
blastoderm filled with yolk, and
the germ-band arising by rapid proliferation
at one point— The resistance of the
yolk being less than the optimal resistance
of the tightly fitting chorion and vitelline
membrane on the one hand, combined
with the amphimal resistance of the
extra-embryonal blastoderm on the other,
the germband is forced to migrate — The
invagination is favored by the displacement
of yolk during its ingestion and
absorption of the growing embryo— We may
suppose that the invagination will
result in the formation of the amnio-
-cervical fold, assumed in dispute and
precise character in different groups of

insects ——

It would be an extremely nice problem
to determine into how many different
& accuracy the mechanical forces
at work in an insects egg when
the amniotal fold arises, and
still more difficult to be able to
predict what must happen as
a result of their action — The observations only make this evident,
and can not, in any sense, it seems
to me, be accepted as an adequate
explanation of the origin of the amnion
of insects —

It seems sufficient to recall the
fact that there is no amnion among
the Crustacea, nor among the Myriopoda
or Aptenygota, and that it is lacking
in certain of the higher insects — Apparently

the same conditions & forms are brought
& view in the Entomostraca, Amphipoda & Stomatopoda it is claimed
& force the investigations which form the
membranes of the Stomata — But no
ommins is found in any of these
forms — It will hardly be claimed that
the imaginations which occur in the spindly
perforating cells of the cleaved blasto-
-derm are the direct result of mechanical
strains — The indirect other factors in
their origin, which I claim are obe-
-dient to the law above — —
In the highly specialized insects that
entirely lack an ommins, its function
& appear to grow more marked — Here,
within the same group the are
forms which, in the face of the
facts above stated as efficient &

produce the phenomena, from none —
I may say here that my own observations on the Limits do not support Wheeler's view —
The same rise is in all probability, as I have tried to show, not only the result of a rapid precipitation but also of a concentration or rendering of alk towards the ground when it is first sine — The same tendency has been shown to be found in the formation of the first rudiment of the embryo in the insect, and in fact throughout — Is the phenomena in no way connected with the origin of the amniotic fold? It is a factor of a very important nature from the view taken by Wheeler but may be equally if not more important — I can't at the case the origin of the membrane can not be so strictly traced to simple conditions of pressure —

a doubt on them. That, though Weismann has enumerated some of the most important mechanical forces found in the egg & embryo, he must be mistaken in considering them the most important factors in the origin of organic structures — This is adaptiveness —

It may be admitted that in the ancestors of amniotic insects the physical constitution of the egg was favorable to the origin of an amnion, but before it could arise a further condition seems important, a necessity for such a structure must be felt — Such a problem may with great probability be greatly spoken of as a mechanical one in its ultimate sense — We are disposed accustomed to regard all natural phenomena as having, we all postulate, fundamentally a physico-chemical explanation —

But granting this, when we attempt to

to explain the origin of a structure account must be taken of all the circumstances both mechanical & physiological. Both these are grounds for we have said the factors without which no variation would appear — The additional influences leading to the origin of a variation in the winged insect, must then be the conjunction of certain physico-chemical forces not brought into play in the case of the asexual (or Enstacek) which are not subtle to be detected except in most general terms — We can only indicate their presence by saying that the nascent structure must be a response to a lack of adjustment of the organism to its environment — The mechanical nature of the problem can not, I think, be stated in more

definite manner than as follows: In some cases (perhaps for protection against injury as Poncelet and Heitz suggest) it became a necessity that the superficial germ-band of the ancestral Metazoa should be covered on some sector in advance — the conditions in it of long favorable for the formation of such a membrane, when the environmental influences became appreciably modified as ammonia was formed by a polchus & a portion of the small disc broke the area as an adaptation to these influences — Embryos in which the disc not covered were eliminated — Then some one among the higher insects as adaptations & special conditions the early completion of this process became

less important, such as a few cells the
least of the degeneration and disappearance
of the nucleus —

P. S. The figures to illustrate this thesis
are submitted separately, as I
am obliged to keep them for
printing —

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Vita –

Thomas Jefferson Thomas was born in Baltimore – Md. August 6th 1868 –

He received his elementary education at the late Mr Jesse J. Carey's school — In 1887 he entered the Johns Hopkins University, selecting the Chemical-Biological course and received the degree of Bachelor of Arts in 1890 at that institution —

On entering as a candidate for the degree of Doctor of Philosophy, he selected Animal-Morphology as his principal subject with Physiology and Botany as first and second subordinates respectively — While pursuing his graduate work he held the position of assistant in Histology, assistant in Zoology, University scholar, and Fellow in Zoology, and during the past year was Johns Hopkins Fellow in Zoology —